Tree Species and Soil Textural Controls on Carbon and Nitrogen Mineralization Rates

Christian P. Giardina,* Michael G. Ryan, Robert M. Hubbard, and Dan Binkley

ABSTRACT

Terrestrial ecosystem models assume that high quality litter leads to the formation of high quality organic C and N in mineral soil, and that increased soil clay content decreases soil C and N mineralization rates. Few studies in forests, however, have examined the effects of initial litter quality and clay content on C mineralization rates (g C kg^{-1} soil C) and net N mineralization rates (g N kg^{-1} soil N) in soil. We used 16-mo laboratory incubations of mineral soil sampled from stands of lodgepole pine (*Pinus contorta* Dougl. ex loud ssp. *latifolia* Englem. ex S. Wats.) and aspen (*Populus tremuloides* Michx.) that varied in clay content (70 to 390 g kg^{-1} soil) to examine how soil C and N mineralization rates relate to initial litter quality and soil texture. Aspen litter quality (C/N = 52–71; lignin/N = 26) was higher than pine litter quality (C/N = 82–111; lignin/N = 40–57), but pine soils released an average of 238 g C kg^{-1} soil C over 16 mo compared with 103 g C kg^{-1} soil C for aspen soils. Higher microbial biomass (mg kg^{-1} soil C) under pine also indicates that pine soil C was of higher quality than aspen soil C. Net N mineralization rates did not relate to species or to soil C mineralization rates, and neither C nor N mineralization rates were related to soil clay content.

The mineralization of soil organic C and N are important processes regulating the functioning of natural and managed ecosystems (Tiessen et al., 1994; Johnson, 1995). Because most detrital C in the terrestrial biosphere is found in mineral soil (Jobbágy and Jackson, 2000), soil C and N mineralization rates also are predicted to control how terrestrial C storage responds to changes in climate or vegetation (Vegetation/Ecosystem Modeling an Analysis Project, 1995). Accurate modeling of soil C and N mineralization rates and their response to a changing environment therefore requires a detailed understanding of the factors that control these biogeochemical processes. The quality of detrital inputs and soil texture are hypothesized to control soil C and N mineralization rates (Wedin and Tilman, 1990; Bonde et al., 1992; Schimel et al., 1994), but relative to the decomposition of fresh litter, little is known about how these variables alter C and N mineralization rates in mineral soil (Bauhus et al., 1998). Few such studies have been conducted in forests where most of the Earth's soil C is stored (Jobbágy and Jackson, 2000).

Christian P. Giardina, Dep. Natural Resources and Environmental Management, Univ. of Hawaii-Manoa, 1910 East-West Rd., Honolulu, HI 96822; Michael G. Ryan, USDA-Forest Service, Rocky Mountain Research Station, 240 West Prospect St., Ft. Collins, CO 80526, and Graduate Degree Program in Ecology and Dep. Forest Science, Colorado State Univ., Ft. Collins, CO 80526; Robert M. Hubbard, USDA-Forest Service, Rocky Mountain Research Station, 240 West Prospect St., Ft. Collins, CO 80526, and Graduate Degree Program in ecology, Colorado State Univ., Ft. Collins, CO 80526; Dan Binkley, Graduate Degree Program in Ecology and Dep. Forest Science, Colorado State Univ., Ft. Collins, CO 80523. Received 12 Sept. 2000. *Corresponding author (giardina@hawaii.edu).

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Three competing hypotheses have been proposed for how initial litter quality influences litter decomposition rates and N release from decomposing litter. The first hypothesis suggests that litter decomposition and N release are positively related to initial litter quality (Fogel and Cromack, 1977; Berg, 1986). In early stages of litter decomposition, C/N may be the best predictor of mass loss and N release (Taylor et al., 1989), while lignin indexes become increasingly important in later stages of decay (Berg, 1986; McClaugherty and Berg, 1987). In the decay filter hypothesis (Melillo et al., 1989), differences in initial litter quality (lignin/N and lignin/cellulose) alter litter decomposition and N release rates in the early stages of litter decomposition. However, as substrate quality converges to some low value during decomposition, initial litter quality has a decreasing influence on late-stage decomposition rates, which instead are controlled by climate, soil texture, and exogenous sources of labile C and nutrients. A third hypothesis suggests that litter decomposition rates and N release may relate inversely to lignin and N-based estimates of initial litter quality. For example, high N content may actually retard litter decomposition rates later in the decomposition process, particularly if lignin levels are also high (Berg, 1986; Fog, 1988; Berg and Matzner, 1997). From these three hypotheses, litter quality can be expected to positively alter, negatively alter, or have no influence on C and N mineralization rates in mineral soil.

In addition to litter quality, clay content is hypothesized to alter soil C and N mineralization rates by binding with organic matter to form soil aggregates that protect soil C and N from heterotrophic soil organisms (Oades, 1988; Six et al., 1999). In situ, ^{13}C field studies show that within a site where climate, litter quality, and biota vary minimally, soil C loss occurs more slowly in clay-sized than in sand-sized soil fractions (Bonde et al., 1992; Desjardins et al., 1994). Despite a near universal pattern of declining decomposition rates with decreasing particle-size, an inverse relationship between C mineralization rates and soil clay content across ^{13}C field studies was not observed (Giardina and Ryan, 2000). In laboratory studies that control temperature and moisture, the effect of clay content on soil C mineralization is weak (Motavalli et al., 1994) or nonexistent (Sørenson, 1981; Hassink et al., 1993; Scott et al., 1996). Evidence for a relationship between soil clay content and net N mineralization is also mixed. At a grassland site, net N transformation rates were lowest in high clay soils (Hassink et al., 1993), but at other sites, clay content did not influence transformation rates (Sørenson, 1981; Motavalli et al., 1995).

The purpose of this study was to examine the effects of litter quality and soil clay content on C and net N

Table 1. Description of stands, sampling locations, and soils used for 16-mo laboratory incubations.

Location	Forest type	Age	Elevation	pH	Clay	Soil C	Soil N	C/N	Soil P
		yr	m			g kg^{-1}		kg kg^{-1}	mg kg
Roosevelt NF	Aspen	70	2740	6.03	310	63	3.5	18.0	650
Fraser Exp. For.	Aspen	80	2820	5.97	390	94	4.6	20.4	858
Routt NF	Aspen	95	2730	6.20	190	53	4.4	12.0	760
Arapaho NF	Aspen	70	2800	5.97	180	77	4.2	18.3	769
Fraser Exp. For.	Aspen	40	2800	6.53	170	47	2.5	18.8	670
Fraser Exp. For.	Aspen	90	2830	5.87	90	32	1.9	16.8	577
Routt NF	Pine	65	2960	4.97	320	47	2.3	20.4	500
Roosevelt NF	Pine	90	3210	5.20	190	27	1.3	20.8	350
Routt NF	Pine	160	2870	4.87	110	11	0.9	12.2	135
Fraser Exp. For.	Pine	70	2830	5.37	110	18	0.8	22.5	343
Fraser Exp. For.	Pine	70	2800	5.53	110	14	1.1	12.7	443
Roosevelt NF	Pine	250	2920	5.57	70	17	0.9	18.9	226

mineralization rates in mineral soils sampled from two subalpine forest types of the central Rocky Mountains. We used 16-mo laboratory incubations of soil sampled from sites with contrasting litter quality inputs (pine or aspen) and a range of soil clay content (70–390 g kg^{-1} soil) to test the hypotheses that C and N mineralization rates are higher in soils receiving inputs of high quality litter, but decrease as clay content increases. Because microbes mediate the effects of species type and clay content on soil C and N mineralization rates, we also examined bacterial and fungal biomass in soil.

MATERIALS AND METHODS

Study Sites

We used differences in species litter quality and site soil texture (Table 1) as natural experiments to test our hypotheses. We selected six closed-canopy lodgepole pine and six closed-canopy aspen sites from among sites in northern Colorado, USA, previously examined by Stump and Binkley (1993). Based on traditional indexes of litter quality, aspen trees produce higher quality leaf litter (less lignin and more N) than do lodgepole pine trees. Aspen roots contain similar concentrations of lignin, but 50% more N than pine roots (Table 2). Further, aspen leaves and roots decomposed more quickly than pine material during 6-mo laboratory incubations (Stump and Binkley, 1993).

The elevation range of lodgepole pine is similar to aspen, but lodgepole pine tends to occur on drier, sandier sites, while aspen tends to occur on wetter, finer textured sites (Peet, 2000). Aspen and pine sites were chosen to represent soil texture endpoints for these forest types (Table 1). In northern Colorado, lodgepole pine and aspen occur on recently disturbed sites, as even-age patches resulting from stand-replacing disturbances, or as mixed-age climax communities (Peet, 2000). Aspen or pine can maintain dominance of a site for several forest generations (Langenheim, 1962); therefore, stand ages presented in Table 1 are minima for site occupation by these forests. Long, cold winters and cool, dry summers characterize all the sites. Mean annual precipitation for the sites ranged from 700 to 850 mm, with most falling as snow (Stump and Binkley, 1993).

Soil Sampling, Analysis, and Incubation

Approximately 2 kg of mineral soil (0–15 cm) were collected from three randomly selected points in stands at each of the 12 sites originally studied by Stump and Binkley (1993). Prior to sampling, forest floor material was removed. The soils were composited by site, and stored for 60 d at 2°C without sieving before chemical analysis and incubation. Immediately prior to analysis and incubation, soils were sieved to 2 mm to remove rocks and roots. Moisture capacity of each soil was then determined by saturating 200 g of soil with water, letting soil drain freely for 24 h on cheesecloth, and weighing a subsample of wetted soil before and after oven drying at 104°C for 24 h. Twelve 200-g samples per soil type (144 in all) were then adjusted to moisture capacity. To improve drainage during leaching, 50-g (wet weight) subsamples of each soil were mixed with 40 g (dry weight) of acid washed quartz sand. The 90-g mixture was placed in Falcon Filter micro-lysimeter cups (Becton Dickinson, Model 7102, Franklin Lakes, NJ) to permit dilute nutrient leaching during the incubation without disturbing the soil, as described by Nadelhoffer et al. (1991). The soil-sand mixture was maintained at field capacity (90 g total weight) throughout the incubation by periodic additions of deionized water. Twelve laboratory replicates of each of the 12 soil types (144 in all) were incubated for 12 mo. From Months 13 to 16, only three of the 12 laboratory replicates per site were used because the other 9 laboratory replicates were used for another experiment.

Soil C mineralization rates were measured by placing microlysimeter cups plus soil into sealed 1-L glass jars with 2 *M* NaOH traps (Anderson, 1982). For the 16-mo incubation period, NaOH traps were sampled and replaced at ~30-d intervals. After addition of 1.0 mL of 0.75 *M* $BaCl_2$, 1.0-mL subsamples of the NaOH were titrated with 1.0 *M* HCl to determine the quantity of NaOH neutralized by absorbed CO_2. Empty microlysimeter cups (blanks) were incubated concurrently throughout the 16-mo incubation period. Changes in base concentration caused by water absorption were estimated by weighing base traps before and after each incubation period and assuming that water absorption caused any increases in weight. Based on CO_2 production, the highest O_2 consumption rate observed was 0.006 mol 31 d^{-1}. Because a 1-L mason jar contains ~0.015 mol O_2, the incubations should have been aerobic for the entire course of study. Incubation temperature was selected to match mean annual air temperature, and was held at 5 ± 1°C throughout the incubation.

Table 2. Litter quality for aspen and lodgepole pine foliage and fine roots.†

Plant Material	N	Lignin	Cellulose	Lignin/N
	g kg^{-1}			kg kg^{-1}
Foliage, aspen	7.3	194	406	28
Foliage, pine	4.5	253	370	57
Fine roots, aspen	8.8	224	444	26
Fine roots, pine	5.5	214	434	40

† Data from Stump and Binkley (1993).

Soil NH_4^+ and NO_3^- were initially extracted from a subsample of each soil by shaking 10 g of sieved, field-moist soil with 100 mL of 2 *M* KCl on a reciprocating shaker for 60 min. Extracts were settled for 30 min, and then passed through preleached (2 *M* KCl) #42 Whatman filters (Whatman International, Kent, England); extracts were stored frozen until analysis (Keeney and Nelson, 1982). To estimate net N mineralization rates and to limit the accumulation of NO_3^- in soils, each of the soil incubations and blanks were leached at the end of Months 4, 8, 12, and 16 with 100 mL of dilute, N-free nutrient solution (Nadelhoffer et al., 1991), and samples were frozen until analysis. At the end of Month 16, a final 2 *M* KCl extraction was performed to remove any mineral N that had not been previously removed by the final dilute nutrient leaching. Sample extracts were analyzed for $NH_4^+$and NO_3^- on a Lachat Instruments AE Flow Injection Autoanalyzer (Lachat Instruments, Milwaukee, WI) according to Lachat Instruments QuikChem Method 12-107-06-2-A (1990) for NH_4^+ and QuikChem Method 12-107-04-1-B (1992) for NO_3^- and nitrite (NO_2^-). To estimate net N mineralization rates for the 16-mo incubations, we made the following calculations: net N mineralization rate equals the NH_4^+ and NO_3^- removed in the final KCl extract plus the NH_4^+ and NO_3^- removed during the four leaching events minus NH_4^+ + NO_3^- removed in the initial, time-zero KCl extract. We assumed no N was lost to dentrification.

Concentrations of C and N in soil were determined on a Leco 1000 CHN analyzer (Leco, St. Joseph, MI) by dry combustion. The Soil Testing Lab at Colorado State University determined soil clay content by hydrometer method (Gee and Bauder, 1986), pH by glass electrode in a 1:2 mixture with deionized water, and total soil P by $NHClO_4$ digestion followed by inductively coupled plasma-spectrometry (Kuo, 1996). At the end of the incubations, a direct count method was used to analyze the three remaining laboratory replicates of each of the 12 soil types for total and active fungal and bacterial biomass (Hendricks et al., 1998). All C, N, and P data are presented on an oven dried soil basis (24 h at 104°C). We express soil C and N mineralization rates as g C or N released per kg soil C or N. Monthly estimates of soil C mineralization are based on soil C content for that month rather than on initial soil C content; the quantity of soil C released during previous months was subtracted from initial soil C. Cumulative release rates are based on soil C content at the beginning of the measurement period in question.

Statistical Analyses

Twelve laboratory replicates for Months 1 to 12 and three laboratory replicates for Months 13 to 16 were used to estimate measurement means for the 12 sites. We used analysis of covariance with species type (aspen or pine) as a fixed factor ($n = 6$) and clay content as the covariate to examine the effects of initial litter quality and clay content on soil C and N mineralization rates, extracted N pools, and microbial biomass (SPSS, version 8.0, Chicago, IL). Patterns of N release during the leaching events were analyzed by repeated measures ANOVA with species and clay content as fixed factors; soils with <18% clay were classified as low clay, while soils with >18% clay were classified as high clay. Relationships among soil clay content, total C and N content, C and N mineralization rates, and microbial biomass were analyzed by means of simple and multiple linear regression. Data were log transformed when the assumption of homogeneity of variance was not met. In all comparisons, $\alpha = 0.05$ was used to protect against Type I errors.

RESULTS

Soil Carbon Mineralization Rates and Soil Carbon Content

Throughout the incubation, C mineralization rates (g C kg^{-1} soil C) were significantly higher in pine than in aspen soils (Fig. 1). At the end of the first 152 d of incubation, cumulative soil C release for pine was 136 g C kg^{-1} soil C compared with 51 g C kg^{-1} soil C for aspen ($P < 0.01$; Fig. 2). Differences between species persisted throughout the incubation; from Day 377 to 483, cumulative soil C release for pine was 22 g C kg^{-1} soil C compared with 12 g C kg^{-1} soil C for aspen ($P < 0.01$; Fig. 2). By the end of 16 mo, total soil C release for pine was 238 g C kg^{-1} soil C compared with 103 g C kg^{-1} soil C for aspen ($P < 0.01$). In contrast, C loss kg^{-1} soil over 16 mo did not differ between species (pine: 4.58 g C kg^{-1} soil; aspen: 6.14 g C kg^{-1} soil; $P = 0.74$).

Cumulative soil C mineralization rates declined with increasing soil clay content ($P = 0.04$), but a near signifi-

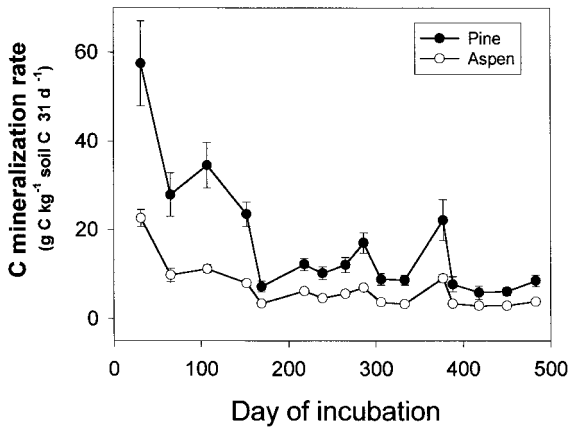

Fig. 1. Means with standard errors for soil C mineralization rates (g C kg^{-1} soil C 31 d^{-1}), which is total soil C release normalized for initial differences in soil C content and adjusted each month for losses of soil C in previous months ($n = 6$).

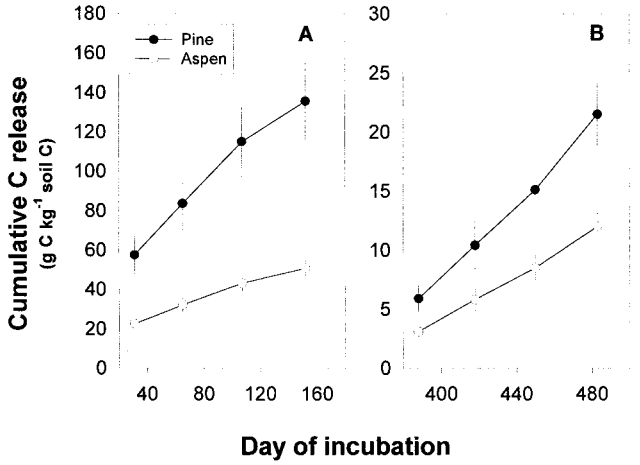

Fig. 2. Means with standard errors for cumulative C release (g C kg^{-1} soil C) from pine and aspen soils ($n = 6$). (A) shows cumulative soil C release during the first 152 d of incubation. (B) shows cumulative soil C release during the last 130 d of incubation.

cant interaction between species type and clay content ($P = 0.06$) suggests that the effect of clay on soil C mineralization rates differed between species. Linear regression analyses showed that within each species total C release did not relate to soil clay content (pine: $R^2 = 0.51$, $P = 0.11$; aspen: $R^2 = 0.14$, $P = 0.46$; Fig. 3A). Within species, soil C content was strongly related to soil clay content (pine: $R^2 = 0.91$, $P < 0.01$; aspen: $R^2 = 0.67$, $P = 0.05$; Fig. 3B), and in a multiple linear regression, clay content and species type (as a dummy variable) explained nearly all of the variation in soil C content ($R^2 = 0.89$, $P < 0.01$).

Net Nitrogen Mineralization Rates and Total Soil Nitrogen Content

More NH_4^+ (g N kg^{-1} soil N) was released from pine than from aspen soils during the four leaching events ($P < 0.01$; Fig. 4A), and the release of NH_4^+ did not relate to soil clay content ($P = 0.37$). Total NO_3^- (g N kg^{-1} soil N) recovered during the four leaching events did not relate to species type (Fig. 4B) or soil clay content ($P = 0.74$ and $P = 0.32$, respectively). Neither species type nor soil clay content altered total N recovered ($NO_3^- + NH_4^+$) during the four leaching events ($P = 0.55$ and $P = 0.29$, respectively), largely because NO_3^- represented 84% of the N recovered from pine soils and 97% of the N recovered from aspen soils. An interaction between time and species type ($P < 0.01$) in an analysis of repeated measures indicated that patterns of total N release differed between species (Fig. 4C). However, over the 16-mo incubation, net N mineralization rates were unrelated to species (pine: 24.6 g N kg^{-1} soil N; aspen: 28.3 g N kg^{-1} soil N; $P = 0.60$). Net N mineralization rates also were unrelated to soil clay content ($R^2 = 0.02$, $P = 0.68$) or C mineralization rates ($R^2 = 0.08$, $P = 0.37$). Species type and soil clay content explained most of the variation in soil N content ($R^2 = 0.85$, $P < 0.01$).

Microbial Biomass

Analysis of covariance showed that pine soil C supported more active fungal, total active, and total bacterial biomass (mg biomass kg^{-1} soil C) than did aspen soil C ($P = 0.03$, $P = 0.01$, and $P = 0.01$, respectively; Fig. 5). Higher levels of active bacterial biomass in pine soils were nearly significant ($P = 0.07$). Total fungal biomass (97% of total microbial biomass) was higher in pine soils ($P = 0.03$), but a species by clay content interaction ($P = 0.04$) indicated that the effect of species varied with clay content. Active fungal biomass increased linearly with soil clay content ($P = 0.04$). Total active biomass, total bacterial biomass, and total fungal biomass increased with soil clay content, but not significantly ($P = 0.07$, $P = 0.06$, $P = 0.10$, respectively). Active bacterial biomass did not relate to soil clay content ($P = 0.17$). Ratios of active fungi/active bacteria were higher in pine than in aspen soils (3.7 and 0.5,

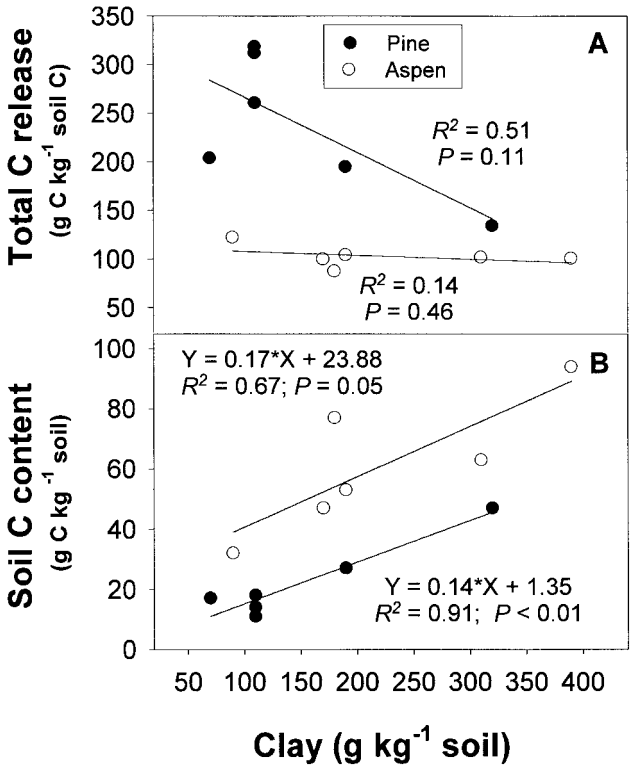

Fig. 3. (A) Relationship between total C release (g C kg^{-1} soil C) over 16 mo and soil clay content (g kg^{-1} soil) for pine and aspen soils ($n = 6$); (B) Relationship between soil C content (g C kg^{-1} soil) and soil clay content (g kg^{-1} soil) for pine and aspen soils ($n = 6$). Regression equations are from linear regression analyses.

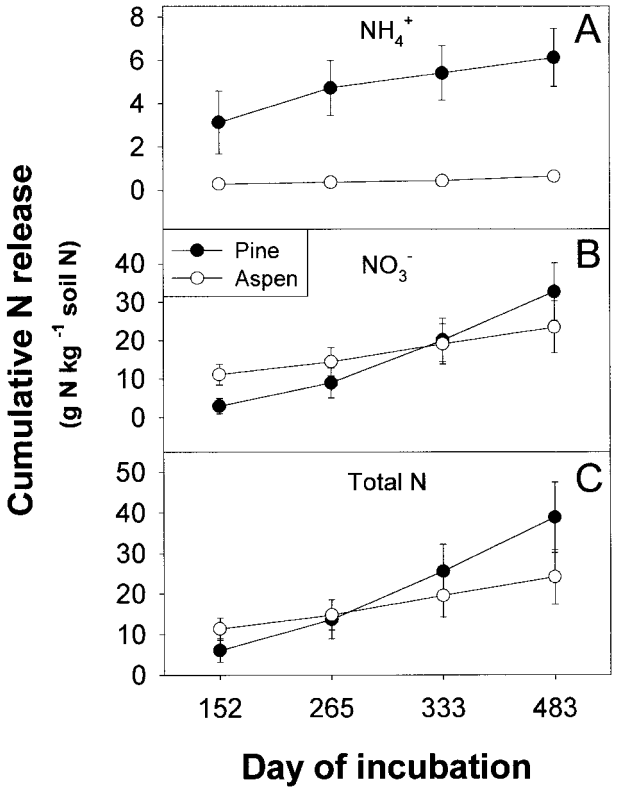

Fig. 4. (A) Means with standard errors for 16 mo cumulative release of NH_4^+ (g N kg^{-1} soil N) from mineral soil sampled from pine and aspen stands during the four leaching events ($n = 6$); (B) Cumulative release of NO_3^- (g N kg^{-1} soil N); (C) Cumulative release of total mineral N (g N kg^{-1} soil N).

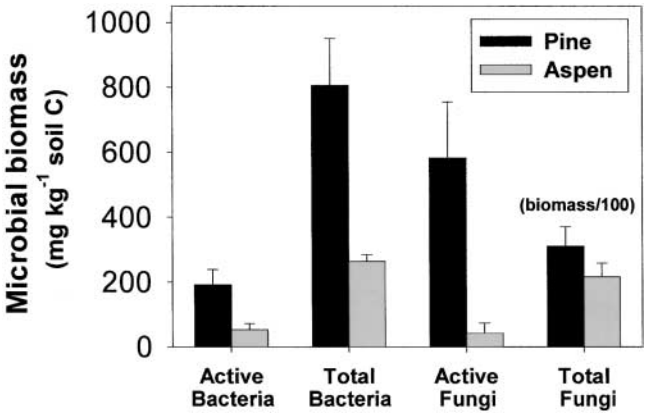

Fig. 5. Means with standard errors for total quantities of active bacterial, total bacterial, active fungal, and total fungal biomass (mg kg^{-1} soil C) in pine and aspen soils (n = 6). Total fungal biomass was divided by 100 to fit the data on the graph.

respectively, $P < 0.01$), and increased with soil clay content (Fig. 6).

DISCUSSION

Species Type, Soil Carbon Mineralization Rates, and Soil Carbon Content

Terrestrial ecosystem models use lignin and N-based indexes of initial litter quality to predict the effects of plants on the size and quality of soil C pools (Vegetation/Ecosystem Modeling and Analysis Project, 1995). However, the influence of initial litter quality on late-stage decomposition rates remains poorly understood because the dramatic changes in substrate quality that occur through the decomposition process have received only limited attention (Couteaux et al., 1995; Prescott et al., 2000). Our data do not support the hypothesis that litter quality positively influences soil C quality (C mineralization rates, microbial biomass), nor the hypothesis that soil C quality is unrelated to litter quality (Melillo et al., 1989). In contrast to what ecosystem models would predict, soil C mineralization rates for pine exceeded those for aspen throughout the incubation (Fig. 1).

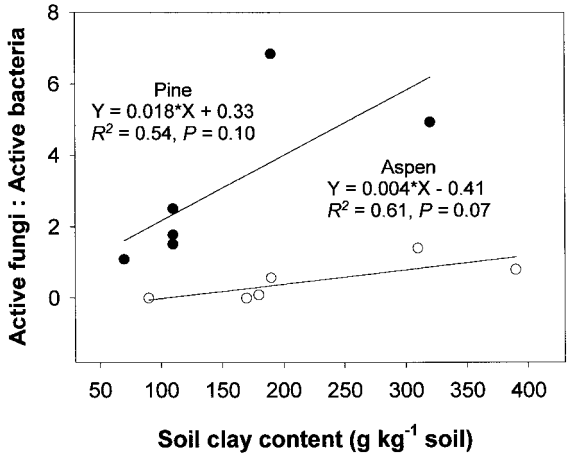

Fig. 6. Relationships between the ratio of active fungi/active bacteria (kg kg^{-1}) and soil clay content (g kg^{-1} soil) for pine and aspen soils (n = 6), across gradients of soil clay content. Regression equations are from linear regression analyses.

Our results are consistent with long-term litter decomposition studies showing that rapid decomposition rates for high quality litter are typically not sustained. In later stages of litter decay, decomposition rates for high quality litter may slow down more rapidly than do rates for low quality litter (Berg, 1986; Prescott et al., 2000). For example, Berg (1986) found that low N content Scot's pine (*Pinus sylvestris* L. Dict. Gard) litter decomposed more slowly in the first two years than high N content Scot's pine litter, but after two years, decomposition rates for the high N content litter declined while decomposition rates for low N content litter continued unchanged. By Year 3, total mass loss and lignin mass loss for low N content litter had surpassed losses for high N content litter (Berg, 1986). Similarly, Prescott et al. (2000) found that first year mass loss for lodgepole pine litter was lower than for aspen litter (30% and 40%, respectively), but by Year 2, differences had disappeared (50%), and by Year 4, mass loss for pine had surpassed aspen (70% and 60%, respectively). Overall, high quality litter from broad leaved trees decomposed more quickly in the first two years compared with conifer litter, but in subsequent years, mass loss for conifer litter often surpassed broad leaved litter (Prescott et al., 2000). In line with these results, Kaye et al. (2000) reported that soil C of grass origin decomposed more slowly when sites were planted to *Albizia falcataria* (L.) Fosberg, a N-fixing tree that produces high quality litter, than when planted to *Eucalyptus saligna* Sm., a similarly fast-growing tree that produces relatively low quality litter. Berg (1986) hypothesized that inverse relationships between litter quality and decomposition were caused by: high N availability inhibiting lignase production or activity; low quality lignin occurring in overall high quality litter; or, decomposition of high N litter leading to the formation of organic matter that is more resistant to decay than organic matter formed from low N content litter.

At the end of our incubations, pine soil C supported microbial communities with a higher proportion of active fungi to active bacteria (Fig. 6). Because certain groups of fungi decompose low quality substrates more effectively than do bacteria (Paul and Clark, 1996), the fungi dominated communities in pine soils may decompose the low quality remains and byproducts of litter decomposition more effectively than the bacteria dominated communities in aspen soils. Conversely, high quality aspen litter may select for organisms that are adapted to higher quality litter, but would do poorly with the low quality remains and byproducts of aspen litter decomposition. Hence, the apparent negative effect of high litter quality on soil C mineralization rates may reflect the influence of tree species on the composition of soil microbial communities.

The C/N of soil did not explain species differences in soil C mineralization rates. Soil C/N did not differ between species (pine: 20.4; aspen: 17.4, $P = 0.81$), and was unrelated to both C/N of initial litter ($P = 0.75$;

Tables 1 and 2) and soil C mineralization rates (pine: $R^2 = 0.33$, $P = 0.23$; aspen: $R^2 = 0.07$, $P = 0.60$). While soil C/N has been used to index soil C quality (Parnas, 1976; Schimel et al., 1994), soil C/N was a poor predictor of C mineralization rates across our sites.

Soil Clay Content, Soil Carbon Mineralization Rates, and Soil Carbon Content

In line with previous studies (Sørenson, 1981; Hassink et al., 1993; Motavalli et al., 1994; Scott et al., 1996), soil C availability was unrelated (aspen) or weakly related (pine) to soil clay content. Variation in climate is unlikely to have masked a relationship between soil C mineralization rates and clay content because climate was similar across sites (Stump and Binkley, 1993). Secondary indexes of soil C quality (microbial biomass and composition) showed mixed results. After 16 mo of incubation, most measures of microbial biomass were unrelated to soil clay content, suggesting that C quality did not vary with clay content (Bauhus et al., 1998). In contrast, analysis of covariance showed that the ratio of active fungi/active bacteria increased with clay content ($P = 0.03$; Fig. 6), suggesting lower soil C quality in high clay soils.

Despite a weak relationship with soil C mineralization rates, soil clay content was a strong predictor of soil C content across our sites (Fig. 3B). These findings appear contradictory, but soil clay content can influence plant productivity (Pastor et al., 1984), and higher soil C content in high clay soils may represent an effect of clay on detritus production rather than an effect on soil C mineralization rates. For example, soil texture can influence water holding capacity and nutrient availability, both of which can influence plant productivity. Similarly, Sørenson (1981) found that while high clay soils retained more ^{14}C labeled cellulose than low clay soils, with differences established in the first 10 d of incubation, soils that retained more cellulose also mineralized proportionally more cellulose over the 4 yr incubation.

Net Nitrogen Mineralization Rates

Large differences between pine and aspen litter quality did not lead to species differences in soil C/N or net N mineralization rates ($P = 0.81$ and $P = 0.68$, respectively). These results are consistent with the decay filter hypothesis (Melillo et al., 1989): early in the decomposition process, low quality litter will release less N than high quality litter because available nutrients are immobilized more rapidly by microbes decomposing low quality, nutrient poor litter. As the quality of diverse litter types converges during decomposition, the influence of initial litter quality on N release should also decline. In contrast to soil N mineralization rates, NH_4^+ was leached at higher rates from pine than aspen soils (Fig. 4A), possibly because abiotic fixation or microbial competition for NH_4^+ were greater in aspen soils. Overall, differences in leached NH_4^+ were small relative to mineralization rates. Cumulative N release increased more rapidly in pine than in aspen soils, suggesting that species differences in N mineralization rates may have emerged had the incubations continued.

Previous studies have shown mixed effects of initial litter quality on net N mineralization rates. In a common garden experiment with perennial grasses, increasing litter quality led to increased net N mineralization rates kg^{-1} soil N (Wedin and Tilman, 1990). In a common garden study with trees, Scott (1998) found that soils under European larch (*Larix deciduo* P. Mill.), which had the highest leaf litter and root quality of five trees examined, had the highest net N mineralization rates kg^{-1} soil N. In contrast, red oak soils had moderate N mineralization rates, but red oak roots and leaf litter were lowest and second lowest in quality.

The decay filter hypothesis predicts that soil texture, climate, and new sources of labile C will control N release in later stages of litter decomposition (Melillo et al., 1989). Across our sites, soil N mineralization rates did not relate to soil clay content, despite constant temperature and moisture during the incubation, and no inputs of labile C. Clay content did not influence quantities of N leached from soil, and analysis of repeated measures showed that clay content did not alter patterns of N release ($P = 0.23$). Our findings are consistent with two long-term studies reporting no relationship between N mineralization rates and soil clay content (Sørenson, 1981; Motavalli et al., 1995), but conflict with a grassland study reporting lower N mineralization rates in high clay soils (Hassink et al., 1993).

Most N in soil is covalently bound to soil C, and the fate of soil N is assumed to follow that of soil C (Schimel et al., 1994; Paul and Clark, 1996). In our study, N mineralization rates were unrelated to soil C mineralization rates. That our estimates of N mineralization represent net rates (i.e., the balance of gross mineralization and immobilization processes in soil) while estimates of soil C mineralization represent gross rates, could explain the poor relationship between N and C mineralization rates. Hart et al. (1994) showed that gross N transformation rates can vary closely with CO_2 release during long-term incubations ($r^2 = 0.97$), but that net N mineralization rates can correlate poorly with gross N transformation rates. If soil C mineralization rate is a good predictor of gross N transformation rates across our soils, then gross N transformations rates would be higher in pine than in aspen soils, but would not vary with soil clay content.

CONCLUSIONS

Based on short-term litter decomposition studies (1 to 2 yr), ecosystem models identify C/N and lignin/N as important predictors of soil C formation and mineralization. Our results suggest, however, that these relationships may be relevant only over the time scales from which they were developed. For the pine and aspen soils compared here, low quality litter resulted in high quality soil C, and faster mineralization of pine C appears to be the explanation for the lower C content of pine soils. Similarly, while large-scale relationships between soil C

and clay content are used to make inferences about how soil C mineralization rates are altered by soil clay content, we found that despite a strong relationship between soil C and clay content, clay was a weak predictor of soil C and N mineralization rates. While in agreement with previous incubation and cross-site comparison studies examining the effects of soil clay content on C mineralization rates, these results conflict with ^{13}C-based particle-size fractionation studies at individual sites reporting a strong influence of soil texture on C turnover. Overall, our results suggest that current assumptions about litter quality and soil textural controls on soil C formation and turnover need to be reevaluated.

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REFERENCES

Anderson, J.P.E. 1982. Soil respiration. p. 831–871. *In* A.L. Page (ed.) Methods of soil analysis. Part 2. 2nd ed. ASA and SSSA, Madison, WI.

Bauhus, J., D. Pare, and L. Cote. 1998. Effects of tree species, stand age and soil type on soil microbial biomass and its activity in a southern boreal forest. Soil Biol. Biochem. 30:1077–1089.

Berg, B. 1986. Nutrient release from litter and humus in coniferous forest soils—A mini review. Scand. J. For. Res. 1:359–369.

Berg, B., and E. Matzner. 1997. Effect of N deposition on decomposition of plant litter and soil organic matter in forest systems. Environ. Rev. 5:1–25.

Bonde, T., B.T. Christensen, and C.C. Cerri. 1992. Dynamics of organic matter as reflected by natural ^{13}C abundance in the particle size fractions of forested and cultivated Oxisols. Soil Biol. Biochem. 24:275–277.

Couteaux, M.-M., P. Bottner, and B. Berg. 1995. Litter decomposition, climate and litter quality. TREE 10:63–66.

Desjardins, T., F. Andreux, B. Volkoff, and C.C. Cerri. 1994. Organic carbon and ^{13}C contents in soils and soil size fractions, and their changes due to deforestation and pasture installation in eastern Amazonia. Geoderma 61:103–108.

Fog, K. 1988. The effect of added nitrogen on the rate of decomposition of organic matter. Biol. Rev. 63:433–462.

Fogel, R., and K. Cromack, Jr. 1977. Effect of habitat and substrate quality on Douglas fir litter decomposition in western Oregon. Can. J. Bot. 55:1632–1640.

Gee, G.W., and J.W. Bauder. 1986. Soil particle size. p. 383–411. *In* A. Klute (ed.) Methods of soil analysis. Part 1. 2nd ed. ASA and SSSA, Madison, WI.

Giardina, C.P., and M.G. Ryan. 2000. Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. Nature 404:858–861.

Hart, S.C., G.E. Nason, D.D. Myrold, and D.A. Perry. 1994. Dynamics of gross nitrogen transformations in an old-growth forest: The carbon connection. Ecology 75:880–891.

Hassink, J., L.A. Bouwman, K.B. Zwart, J. Bloem, and L. Brussard. 1993. Relationships between soil texture, physical protection of organic matter, soil biota, and C and N mineralization in grassland soils. Geoderma 57:105–128.

Hendricks, C.W., M.T. Holmes, and E.R. Ingham. 1998. Foodweb methodology to assess ecological effects of anthropogenic stressors in soil. Trends Soil Sci. 2:181–189.

Jobbágy, E.G., and R.B. Jackson. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecol. Applic. 10:423–436.

Johnson, D.W. 1995. Role of carbon in the cycling of other nutrients in forested ecosystems. p. 299–328. *In* W.W. McFee and J.M. Kelly (ed.) Carbon forms and functions in forest soils. SSSA, Madison, WI.

Kaye, J.P., S.C. Resh, M.W. Kaye, and R.A. Chimner. 2000. Nutrient and carbon dynamics in a replacement series of *Eucalyptus* and *Albizia* trees. Ecology 81:3267–3273.

Keeney, D.R., and D.W. Nelson. 1982. Nitrogen—Inorganic forms. p. 643–698. *In* A.L. Page (ed.) Methods of soil analysis. Part 2. 2nd ed. ASA and SSSA, Madison, WI.

Kuo, S. 1996. Phosphorus. p. 869–919. *In* D.L. Sparks (ed.) Methods of soil analysis. Part 3. Chemical methods. SSSA Book Ser. 5. SSSA, Madison, WI.

Lachat Instruments. 1990. Analysis of low concentration of ammonum in water. QuikChem Method 12-107-06-2-A, Lachat Instruments, Milwaukee, WI.

Lachat Instruments. 1992. Analysis of low concentration of nitrate and nitrite in water. QuikChem Method 12-107-06-2-B, Lachat Instruments, Milwaukee, WI.

Langenheim, J.H. 1962. Vegetation and environmental patterns in the Crested Butte area, Gunnison County, Colorado. Ecol. Monogr. 32:249–285.

McClaugherty, C., and B. Berg. 1987. Cellulose, lignin and nitrogen concentrations as rate regulating factors in late stages of forest litter decomposition. Pedobiologia 30:101–112.

Melillo, J.M., J.D. Aber, A.E. Linkins, A. Ricca, B. Fry, and K.J. Nadelhoffer. 1989. Carbon and nitrogen dynamics along the decay continuum: Plant litter to soil organic matter. Plant Soil 115:189–198.

Motavalli, P.P., C.A. Palm, E.T. Elliott, S.D. Frey, and P.C. Smithson. 1995. Nitrogen mineralization in humid tropical forest soils: Mineralogy, texture, and measured nitrogen fractions. Soil Sci. Soc. Am. J. 59:1168–1175.

Motavalli, P.P., C.A. Palm, W.J. Parton, E.T. Elliott, and S.D. Frey. 1994. Comparison of laboratory and modeling simulation methods for estimating soil carbon pools in tropical forest soils. Soil Biol. Biochem. 26:935–944.

Nadelhoffer, K.J., A.E. Giblin, G.R. Shaver, and J.A. Laundre. 1991. Effects of temperature and substrate quality on element mineralization in six arctic soils. Ecology 72:242–253.

Oades, J.M. 1988. The retention of organic matter in soils. Biogeochemistry 5:35–70.

Parnas, H. 1976. A theoretical explanation of the priming effect based on microbial growth with two limiting substrates. Soil Biol. Biochem. 8:139–144.

Pastor, J., J. Aber, C. McClaugherty, and J. Melillo. 1984. Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. Ecology 65:256–268.

Paul, E.A., and F.E. Clark. 1996. Soil Microbiology and Biochemistry. Academic Press, San Diego, CA.

Peet, R.K. 2000. Forests and meadows of the Rocky Mountains. p. 75–122. *In* M.G. Barbour and W.D. Billings (ed.) North American terrestrial vegetation. 2nd ed. Cambridge Univ. Press, Cambridge, UK.

Prescott, C.E., L.M. Zabek, C.L. Staley, and R. Kabzems. 2000. Decomposition of broadleaf and needle litter in forests of British Columbia: Influences of litter type, forest type and litter mixtures. Can. J. For. Res. 30:1742–1750.

Schimel, D.S., B.H. Braswell, E.A. Holland, R. McKeown, D.S. Ojima, T.H. Painter, W.J. Parton, and A.R. Townsend. 1994. Climatic, edaphic, and biotic controls over storage and turnover of carbon in soils. Global Biogeochem. Cycles 8:279–293.

Scott, N.A. 1998. Soil aggregation and organic matter mineralization in forest and grasslands: plant species effects. Soil Sci. Soc. Am. J. 62:1081–1089.

Scott, N.A., C.V. Cole, E.T. Elliott, and S.A. Huffman. 1996. Soil textural control on decomposition and soil organic matter dynamics. Soil Sci. Soc. Am. J. 60:1102–1109.

Six, J., E. Elliott, and K. Paustian. 1999. Aggregate and soil organic matter dynamics under conventional and no-tillage systems. Soil Sci. Soc. Am. J. 63:1350–1358.

Sørenson, L.H. 1981. Carbon-nitrogen relationships during the humification of cellulose in soils containing different amounts of clay. Soil Biol. Biochem. 13:313–321.
Stump, L.M., and D. Binkley. 1993. Relationships between litter quality and nitrogen availability in Rocky Mountain forests. Can. J. For. Res. 23:492–502.
Taylor, B.R., D. Parkinson, and W.F.J. Parsons. 1989. Nitrogen and lignin content as predictors of litter decay rates: A microcosm test. Ecology 70:97–104.
Tiessen, H., E. Cuevas, and P. Chacon. 1994. The role of soil organic matter in sustaining soil fertility. Nature 371:783–785.
Vegetation/Ecosystem Modeling and Analysis Project. 1995. Vegetation/ecosystem modeling and analysis project: Comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem response to climate change and CO_2 doubling. Global Biogeochem. Cycles 9:407–437.
Wedin, D.A., and D. Tilman. 1990. Species effects on nitrogen cycling: A test with perennial grasses. Oecologia 84:433–441.

DIVISION S-7—NOTES

LONG-TERM PATTERNS IN FOREST-FLOOR NITROGEN-15 NATURAL ABUNDANCE AT HUBBARD BROOK, NH

L. H. Pardo,* H. F. Hemond, J. P. Montoya, and T. G. Siccama

Abstract

To test the hypothesis that $\delta^{15}N$ in the forest floor remains constant over time, we measured $\delta^{15}N$ in forest-floor samples from 1969, 1978, 1987, and 1992 at the reference watershed, W6, at the Hubbard Brook Experimental Forest (HBEF), New Hampshire. The $\delta^{15}N$ of the Oa horizon increased significantly ($P < 0.05$) from 3.00‰ in 1969 to 4.89‰ in 1978, then decreased significantly to 3.81‰ in 1987 and remained near that level in 1992. In the Oie horizon, $\delta^{15}N$ increased significantly from 0.17‰ in 1969 to 0.91‰ in 1978 and remained at the higher level for the later years. Thus $\delta^{15}N$ was not at steady state in either the Oie or Oa horizon for the period 1969 to 1992 in the reference watershed. These data suggest that even relatively short-term disruptions of the N cycle (either by anthropogenic or natural disturbance) can alter the $\delta^{15}N$ in the forest floor, and should be considered in evaluating natural abundance data.

Natural abundance of ^{15}N has been used to help evaluate N cycling and N losses (Johanisson and Högberg, 1994; Austin and Vitousek, 1998; Emmett et al., 1998), to compare plant species patterns of N uptake (Nadelhoffer et al., 1996), and to compare land-use history (Piccolo et al., 1994). An underlying assumption that soil $\delta^{15}N$ is at steady state is made in many studies, including laboratory experiments evaluating the change in soil $\delta^{15}N$ in response to mineralization and nitrification (Nadelhoffer and Fry, 1988), comparisons of a N deposition gradient in the NITREX study (Emmett et al., 1998), and models (Shearer et al., 1974; Hobbie et al., 1999). Although it is reasonable to assume that the $\delta^{15}N$ in the mineral soil changes very little over time because of the large pool size and long residence time, the steady-state assumption in the forest floor has not been established.

The stable N isotope ratio (^{15}N to ^{14}N) is useful in ecological research because it records the net effects of N transformations on the soil (Högberg, 1997). Microbially mediated processes discriminate against the heavier ^{15}N, creating products that are depleted in ^{15}N and leaving the source pool enriched in ^{15}N (Mariotti et al., 1981; Shearer and Kohl, 1986). If the depleted product is exported from the soil (via uptake or leaching after nitrification or gaseous losses after denitrification), the remaining soil becomes enriched in ^{15}N (Létolle, 1980; Shearer and Kohl, 1986; Nadelhoffer and Fry, 1994). The fractionation during nitrification, ≈15 to 36‰ (Högberg, 1997), is significantly higher than that during mineralization (≈1‰; Högberg, 1997; Kendall, 1998).

Because litter $\delta^{15}N$ values are consistently lower than soil values, litterfall inputs tend to lower the $\delta^{15}N$ of the forest floor (Fry, 1991; Nadelhoffer and Fry, 1994; Högberg, 1997). Likewise, because soil is typically enriched relative to the atmosphere, N fixation also decreases soil $\delta^{15}N$. Nitrogen fixation incorporates atmospheric N, which has a $\delta^{15}N$ of 0‰, into plant material and subsequently into soil with a fractionation that typically ranges from −1 to +1‰ (Shearer and Kohl, 1986).

Other N fluxes may either deplete or enrich soil ^{15}N; these include deposition and immobilization. The $\delta^{15}N$ of ammonium and nitrate in deposition varies considerably, the former from −14 to 9‰ (Hoering, 1957; Freyer, 1978; Paerl and Fogel, 1994), and the latter from −7 to 6‰ (Hübner, 1986; Garten, 1992; Kendall, 1998; Pardo et al., 1998). At the HBEF, the $\delta^{15}N$ of precipitation nitrate is −2‰ (Pardo, unpublished data, 1996–1998); $\delta^{15}N$ has not been measured for ammonium. Ammonium deposition may be more enriched (Hoering, 1957; Nadelhoffer et al., 1999) or less enriched (Freyer, 1978; Garten, 1992) in $\delta^{15}N$ than nitrate deposition. The effect of N deposition on forest soil, therefore, cannot be predicted a priori. At the HBEF, because nitrate deposition is depleted relative to soil (as is ammonium for the nearest site with data available; Nadelhoffer et al., 1999),

L.H. Pardo, Northeastern Research Station, USDA Forest Service, P.O. Box 968, Burlington, VT 05402; H.F. Hemond, MIT 48-311, 77 Massachusetts Ave., Cambridge, MA 02139; J.P. Montoya, Georgia Institute of Technology, School of Biology, 310 Ferst Dr., Atlanta, GA 30332; T.G. Siccama, Yale School of Forestry and Environmental Science, 370 Prospect St., New Haven, CT 06511. Received 18 Apr. 2000. *Corresponding author (lpardo@fs.fed.us).

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Abbreviations: HBEF, Hubbard Brook Experimental Forest; LOI, loss on ignition; W6, reference Watershed 6.